

VISUAL COMMUNICATION AND SEXUAL SELECTION IN A NOCTURNAL BIRD SPECIES, *CAPRIMULGUS RUFICOLLIS*, A BALANCE BETWEEN CRYPSIS AND CONSPICUOUSNESS

JUAN ARAGONÉS,^{1,2,3} LUIS ARIAS DE REYNA,¹ AND PILAR RECUERDA¹

ABSTRACT.—Cryptic protective mechanisms and the conspicuousness required to communicate result in a conflict of opposing selection. In the Red-necked Nightjar (*Caprimulgus ruficollis*) a nocturnal bird, the use of a restricted signaling strategy provides an appropriate balance between these two selection forces. Conspicuous white wing and tail bands may have been favored by sexual selection in this species. We studied the variation of visual signals and found conspicuousness to be closely related to sex and age, being much higher in males and adults. This variation allows an individual to identify the reproductive status of conspecifics, providing sexual selection a basis to select these visual signals in this and other nocturnal bird species. We believe that a relationship between restricted signaling strategy and sexually selected visual signals may occur in nocturnal species that use visual communication. Received 24 April 1998, accepted 5 Feb. 1999.

Crypsis is one of the more effective anti-predator mechanisms (Baker and Parker 1979). Because it relies on inconspicuousness, its use can conflict with the conspicuousness required for communication. Selection pressure drives populations to address signals among conspecifics (conspicuousness increases at close range) and to conceal them from predators (inconspicuousness or long range crypsis; Butcher and Rohwer 1989). An appropriate balance between crypsis and communication is achieved by the use of restricted signaling, for example, the presence of hidden conspicuous signals in highly specific body zones that are only exhibited in some situations (see Butcher and Rohwer 1989).

In strictly nocturnal birds, which account for less than 3% of all bird species (Martin 1990), the visual channel is assumed to play an insignificant role in communication compared to diurnal birds. However, this is only an assumption and nocturnal birds may use visual signals to communicate more widely than is thought. The Red-necked Nightjar (*Caprimulgus ruficollis*) is a nightbird of open and semi-open habitats that uses sight to capture flying insects. The plumage of caprimulgids is highly cryptic, but includes white spots on wings, tail, and throat. These markings, because of their anatomical location, are only

visible in some contexts (agonistic, antipredator, and sexual displays) when the sender intentionally shows its markings to the receiver (Bent 1940, Mengel 1972, Bruce 1973, Cramp 1985, Fry et al. 1988, Cleere 1998, Aragonés et al. in press). Some caprimulgid species have been reported to show individual variation in spot size and color (Common Nighthawk, *Chordeiles minor*, Selander 1954; Red-necked Nightjar, Beven 1973, Soares 1973; Blackish Nightjar, *C. nigrescens*, Ingels and Ribot 1982). This variation in spots suggests that signal conspicuousness might vary with age and sex.

The objective of this paper is to describe the variation of spots in signal conspicuousness in the Red-necked Nightjar and to examine whether this variation is related to age and/or sex. We hypothesize that if males, especially adult males, show greater conspicuousness in wing and tail bands, then these plumage characters may be sexually selected.

METHODS

We used data from 170 specimens obtained from bird collections at Estación Biológica de Doñana, CSIC ($n = 22$) and from road casualties ($n = 148$) in Córdoba (southern Spain) during the 1986 to 1994 breeding seasons. From this sample we measured the following variables related to conspicuousness. (1) Band size. The wing-band consisted of 3 to 4 spots and the tail-band of 2 to 3 spots. Using a digital caliper, the longer and shorter axis of each spot was measured (± 0.1 mm) and the area for each was calculated. The surface areas of the spots present in the outer primaries of the right wing were summed and recorded as wing-band size and those on right rectrices were summed and recorded as tail-band size. The area of each spot

¹ Dpto. Biología Animal, Univ. de Córdoba, Avda. San Alberto Magno, sn. 14004 Córdoba, Spain.

² Present address: Avda. Cádiz nº 5, 14009-Córdoba, Spain.

³ Corresponding author; E-mail: ba2biani@uco.es

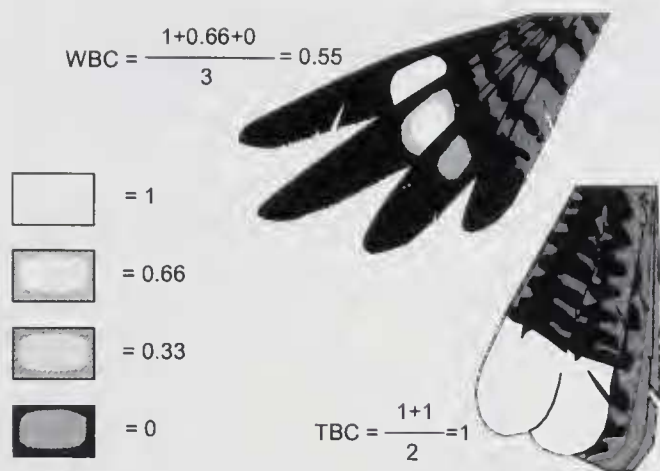


FIG. 1. Wing-band (WBC) and tail-band contrast (TBC), calculated from color and sharpness values of spots forming the bands (1 = maximum contrast value, white spot with sharp contrasting edges, 0 = minimum contrast value, dark spots without sharp contrasting edges).

was indexed by the product of the long and the short axis. (2) Band contrast. Contrast was measured from the color and sharpness of the spots that formed the wing and tail bands. The contrast gradient was established from a reference series formed by four types of spots that were assigned the values 0, 0.33, 0.66 and 1; where 0 denoted the spot with the darkest colour and least sharp contrasted edges, and 1 that with the lightest color and sharpest edges. A given individual can possess spots of different types (depending on color and sharpness variations), so each spot was assigned a value, and a mean index was used for the contrast analysis in wing-band contrast and tail-band contrast which included all spots of the wing and tail (Fig. 1). (3) Uniformity of color spots within a band. Some individuals showed bands consisting of a single type of spot, whereas others had one or two different types; the former were designated "uniform" and the latter "non-uniform". (4) Spot number in wing and tail bands. (5) Band conspicuousness. Band size and contrast values were first log transformed, normalizing the data for the application of parametric statistics and used to calculate a conspicuousness index (C) from the following expression:

$$C = \frac{WBS \times \log(WBC+1) + TBS \times \log(TBC+1)}{WBS + TBS}$$

where WBS = wing-band size, TBS = tail-band size, WBC = wing-band contrast, and TBC = tail-band contrast. This index varied from 0 to 1, with 1 corresponding to maximum conspicuousness. Sex was determined by gonadal dissection. Differences in band size and conspicuousness were analysed by ANOVA and the Tukey test, and differences in the number of spots and their uniformity by means of the *G*-test. Contrast differences were identified by multiple logistic regression, which allows one or more categorical variables (contrast in our case) to be analysed and related to a dependent variable. This method is especially suit-

able for data that are not normally distributed and is more effective than other classifying methods such as discriminant analysis (Press and Wilson 1978; see also Harrell 1986, Schlinger 1990, Fancy et al. 1993). Conspicuousness data were transformed logarithmically for parametric analysis. All analyses were performed using JMP software (version 2, Macintosh computer).

RESULTS

There were significant differences in wing-band size ($F = 31.47$, $df = 3, 90$, $P < 0.001$) and tail-band size ($F = 41.61$, $df = 3, 90$, $P < 0.001$) between sex-age categories. Wing and tail bands were significantly larger in males than in females and larger in adults relative to young. There was a clear trend for band size to increase in an age-sex sequence, both in wing-band (mean young females = 662.3 ± 37.87 SD, $n = 29$; mean adult females = 803.1 ± 52.66 , $n = 15$; mean young males = 986.3 ± 37.24 , $n = 30$; mean adult males = 1210.5 ± 45.61 , $n = 20$) and in tail band (mean young females = 743.4 ± 67.06 , $n = 29$; mean adult females = 1046.4 ± 93.24 , $n = 15$; mean young males = 1428.7 ± 65.93 , $n = 30$; mean adult males = 1852.6 ± 80.75 , $n = 20$). Both variables were found to be positively correlated ($r = 0.67$, $n = 93$, $P < 0.001$).

The multiple logistic regression discriminated between the four age-sex classes in terms of wing-band or tail-band contrast (Table 1). There were significant differences in sex and age for wing-band contrast ($\chi^2_3 = 86.33$, $P < 0.001$, $n = 94$) and tail-band contrast ($\chi^2_3 = 94.21$, $P < 0.001$, $n = 94$). Males and adults always had the largest contrast index both for wing-band and tail-band (Fig. 2). Sharp edges were detected only in males with wing-band or tail-band contrast index close to one because only such spots had sharp edge contrasts. Males showed greater uniformity in wing-band contrast than females, and adults were more uniform than young in this respect. All groups showed uniform tail bands (Table 2).

The presence of four spots on the wing is an exclusive feature of adult males (Table 2); over 45% ($n = 16$) of adult males have the fourth spot. About 80% of adult males also tended to possess three caudal spots ($n = 28$; Table 2). Additional spots on the tail was not significantly different among the other groups (Table 2). The additional wing spot increased

TABLE 1. Parameter estimates of logistic functions derived from multiple logistic regression.

Logistic function parameters	Estimate	Wald test	P
(Young female vs adult female)			
Intercept 1	9.47	17.62	<0.001
Wing-band contrast	-13.22	21.22	<0.001
(Adult female vs young male)			
Intercept 2	7.52	11.51	<0.001
Wing-band contrast	-10.17	14.43	<0.001
(Young male vs adult male)			
Intercept 3	1.63	0.56	>0.05
Wing-band contrast	-1.34	0.32	>0.05
(Young female vs adult female)			
Intercept 1	10.05	23.21	<0.001
Tail-band contrast	-16.03	31.09	<0.001
(Adult female vs young female)			
Intercept 2	8.45	16.36	<0.001
Tail-band contrast	-12.29	20.59	<0.001
(Young male vs adult male)			
Intercept 3	6.09	10.54	<0.001
Tail-band contrast	-6.90	10.20	<0.001

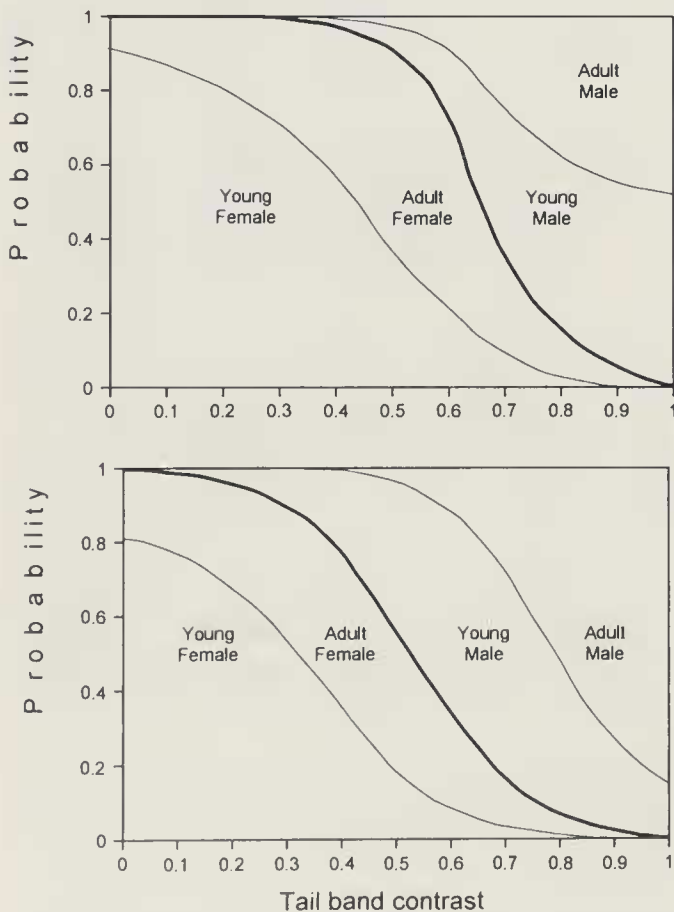


FIG. 2. Heavy line indicates probability of belonging to a sex class as a function of wing-band contrast (WBC) or tail-band contrast (TBC), thin lines indicates probability of belonging to an age class.

the wing-band size of adult males an average of 6% and the tail-band size of adult males an average of 12%. The presence of additional spots on wing and tail increased the overall band area by 9.6% and presumably increased signal conspicuousness. There were significant differences in conspicuousness (Table 2) with regard to age–sex classes, with greater conspicuousness in males and adults.

DISCUSSION

We detected a marked trend for signal conspicuousness to increase with age and in males which was reflected in an increase of contrast, number of spots, wing- and tail-bands area, and uniformity of contrast. The differences in conspicuousness in wing- and tail-bands were related to the age and sex class of the individual. Potentially, these signals let conspecifics evaluate one another in aggressive or reproductive contexts. Signal conspicuousness seemingly involves little energy expenditure but is combined with expensive displays; the combination results in an efficient signal that conveys a much greater amount of information (Hasson 1991). We found that spot number was related to sex and age, but Forero and coworkers (1995) found no statistically significant differences in the average

TABLE 2. Frequency distribution of contrast uniformity, additional spots in bands and conspicuousness index for age-sex groups.

	Female		Male		<i>P</i>
	Young	Adult	Young	Adult	
Contrast uniformity (<i>n</i> = 94)	<i>n</i> = 29	<i>n</i> = 15	<i>n</i> = 30	<i>n</i> = 20	
WBC ^a ($G_3 = 27.29$)	37%	66%	66%	95%	<0.001
TBC ^a ($G_3 = 11.09$)	88%	87%	91%	89%	>0.05
Additional spots (<i>n</i> = 170)	<i>n</i> = 50	<i>n</i> = 31	<i>n</i> = 54	<i>n</i> = 35	
In wing ($G_3 = 40.33$)	0%	0%	0%	55%	<0.001
In tail ($G_3 = 39.85$)	6%	6%	6%	80%	<0.001
Conspicuousness (<i>n</i> = 94)	<i>n</i> = 29	<i>n</i> = 15	<i>n</i> = 30	<i>n</i> = 20	
($F = 71.76$, <i>n</i> = 3, 90)	0.23	0.43	0.43	0.91	<0.001

^a WBC = wing-band contrast, TBC = tail-band contrast.

number of spots between groups of the same species. We believe the addition of new spots has a strong biological significance because it occurs only in adult males as reported by Forero and coworkers (1995), but their method, failed to demonstrate a significant difference.

In the Red-necked Nighthawk increased signal conspicuousness may increase the likelihood of mating (Andersson 1982, Andersson 1992, Saetre et al. 1994), and conspicuous males may have a higher mating success (Payne 1982, Price 1984, Järvi et al. 1987, Harvey

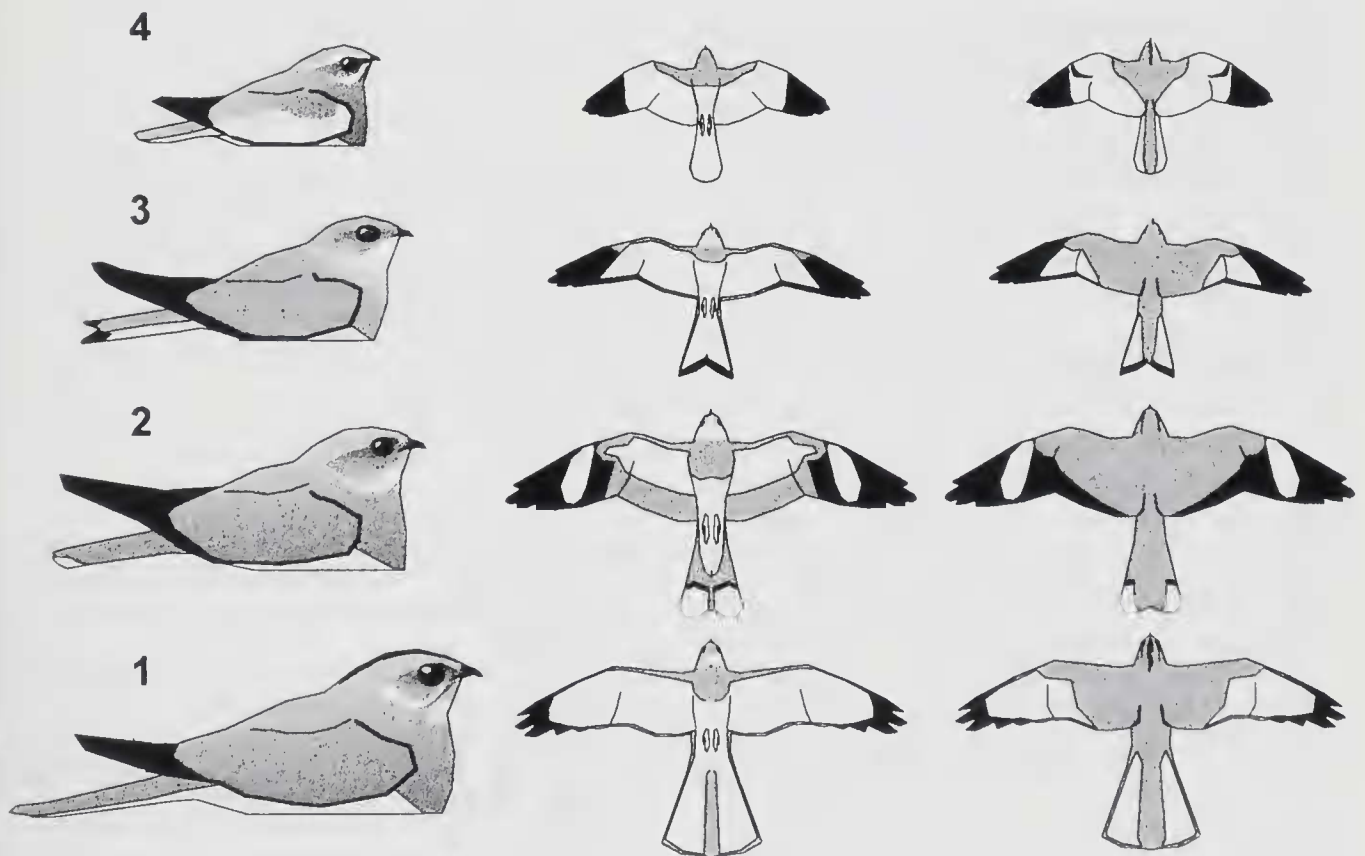


FIG. 3. For restricted signaling strategy to be effective, conspicuous plumage zones (black and white areas in the drawing) must be concealed by cryptic plumage zones (gray areas in the drawing) while at rest. A hypothetical model based on the genus *Caprimulgus* (1) represents the maximum possible conspicuousness for restricted signaling strategy; a larger conspicuous area would defeat the defensive system based on crypsis and hence cancel restricted signaling strategy. The Nacunda Nighthawk (2), the Sand-Colored Nighthawk (3) and the White-Winged Nighthawk (4) use three restricted signaling strategies that are very similar to that of the model, especially the Sand-Colored Nighthawk.

and Bradbury 1991, Sundberg and Larsson 1994). The fact that increased signal conspicuousness was associated with adult males suggests that the signal could be modified by sexual selection (Höglund 1993). For adult males, this signal indicates that those individuals have survived at least two reproductive seasons and, therefore, may reflect a high reproductive quality. In another nocturnal bird species, the Great Snipe (*Gallinago media*) males have white spots on their tails, and females choose the males with the whitest signals (Höglund et al. 1992). This suggests that signal conspicuousness in nocturnal birds could be an effective way of distinguishing between potential mates.

Our results show that in Red-necked Nightjar both sexes possess ornaments, and that in both sexes spots tend to increase in conspicuousness with age. Forero and coworkers (1995) claimed that visual signals increased only in males. We believe that their results are due to a less precise method of measuring spot size.

The restricted signaling strategy allows two scarcely compatible mechanisms to be combined and might occur in many cryptic species of the genera *Burhinus*, *Charadrius* and *Gallinago*, although this has not yet been investigated. For a nocturnal signal, contrast is more important than color, as in the caprimulgids and other species that use restricted signaling strategy with white spots (i.e., *Gallinago media*, Höglund et al. 1992; *Burhinus* spp., Martin 1990, Hayman et al. 1986). Therefore, increasing the amount of white color increases contrast and presumably maximizes the signaling ability. Similar trends of increasing conspicuousness with age have been detected in other caprimulgids (Little Nightjar, *C. parvulus heterurus*, Schwartz 1968; Chuck-Will's-Widow, *C. vociferus*, Rohwer 1971; Blackish Nightjar, Ingels and Ribot 1982; Scrub Nightjar, *C. anthonyi*, Robins and Ridgeley 1994; Nacunda Nighthawk, *Podager nacunda*, Aragonés unpubl. data; Pauraque, *Nyctidromus albicollis*, Aragonés 1997a, b).

From the distribution of visual signals in Red-necked Nightjar (throat, wings, and tail-bands), we developed a model plumage pattern for a nightjar that represents the optimum/maximum distribution of conspicuous areas in

the body (Fig. 3). We subsequently found that the Nacunda Nighthawk and the White-Winged Nightjar (*Caprimulgus candicans*) have patterns that closely resemble our model, and the Sand-colored Nighthawk's (*Chordeiles rupestris*) visual signals patterns are identical with that of the model. All three are gregarious South American species of open or semiopen habitats with sexual variations in wing- and tail-bands (Ffrench 1986, Hilty and Brown 1986, Sick 1993). It is interesting to note that the Sand-colored Nighthawk and the Yellow-billed Tern (*Sterna superciljaris*), two Amazonian species that use the same fluvial habitat, show almost identical visual signal patterns and general appearance (see Sick 1993). This convergent evolution stresses the significance of open and semiopen habitats for restricted signaling strategy evolution. Such habitats are also characterized by other species that employ this strategy, *Burhinus* spp. and the Great Snipe (Hayman et al. 1986). We believe that a relationship between restricted signaling strategy and sexually selected visual signals may occur in nocturnal species that uses visual communication.

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